Fluctuations of visual awareness: Combining motion-induced blindness with binocular rivalry

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Binocular rivalry (BR) and motion-induced blindness (MIB) are two phenomena of visual awareness where perception alternates between multiple states despite constant retinal input. Both phenomena have been extensively studied, but the underlying processing remains unclear. It has been suggested that BR and MIB involve the same neural mechanism, but how the two phenomena compete for visual awareness in the same stimulus has not been systematically investigated. Here we introduce BR in a dichoptic stimulus display that can also elicit MIB and examine fluctuations of visual awareness over the course of each trial. Exploiting this paradigm we manipulated stimulus characteristics that are known to influence MIB and BR. In two experiments we found that effects on multistable percepts were incompatible with the idea of a common oscillator. The results suggest instead that local and global stimulus attributes can affect the dynamics of each percept differently. We conclude that the two phenomena of visual awareness share basic temporal characteristics but are most likely influenced by processing at different stages within the visual system.

Introduction

Experimental paradigms that evoke multistable percepts have attracted considerable interest because they offer a tool for decoupling conscious perception from physical stimulation (Crick & Koch, 1990). In binocular rivalry (BR), for example, the observer's conscious perception fluctuates between incompatible images presented to the left and right eyes, even though retinal stimulation in each eye remains constant (Blake, 2001; Blake & Logothetis, 2002). Similarly, in motion-induced blindness (MIB), a salient target disappears and reappears from conscious perception, sometimes for several seconds at a time, when presented against a global moving mask (Bonneh et al., 2001a). Both phenomena have been used to probe visual awareness because changes in neural responses that correlate with subjective perception have no physical equivalent in the stimulus itself (Crick & Koch, 1990, 1995; Koch, 2004).

Carter and Pettigrew (2003) reported a significant correlation between reversal rates for BR and MIB. They also found that an increase in total disappearance was accompanied by a decrease in appearance, similar to effects of stimulus strength in BR (Levelt, 1965). In addition, if drugs (lysergic acid diethylamide) were administered to individual observers, the distribution of phase durations for both BR and MIB was altered together in a characteristic way. More recently, van Loon et al. (2013) found significant correlations between *gamma*-Aminobutyric acid (GABA) concentration in the visual cortex and phase durations for BR and MIB. However, these correspondences across individual observers do not necessarily imply a single oscillator or common inhibitory mechanism for both phenomena.

In a series of studies, Leopold, Wilke, Maier, and Logothetis (2002) and Maier, Wilke, Logothetis, and Leopold (2003) interrupted bistable perception by periodically inserting intervals with a blank display. They found that alternation rates for various bistable phenomena were dramatically reduced, indicating a strong top-down influence of selective attention on bistable perception. In one experiment in particular, Leopold et al. (2002) introduced MIB to a target stimulus with ambiguous rotation direction and found reduced alternation (stabilization) of perceived rotation direction when interrupted by target disappearance.

Here we employ a related paradigm that can evoke MIB and BR in the same stimulus display. We monitored fluctuating perceptual states while manipulating stimulus characteristics that are known to affect MIB and BR. We hypothesized that if systematic

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manipulation of MIB affects the dynamics of BR and systematic manipulation of BR alters the dynamics of MIB, then both phenomena are coupled and may involve a single oscillator (Carter & Pettigrew, 2003) or common inhibitory mechanism (van Loon et al., 2013).

Alternatively, if we can show that manipulation of MIB has no corresponding effect on the dynamics of BR and that manipulation of BR exerts no corresponding effect on the dynamics of MIB, then this suggests that both phenomena involve different processing while competing for visual awareness (Blake & Logothetis, 2002; Sterzer, Kleinschmidt, & Rees, 2009), involving bottom-up sensory processing (Lee, Blake, & Heeger, 2007) and possibly top-down selective attention (Brascamp & Blake, 2012; Desimone & Duncan, 1995; Kleinschmidt, Büchel, Zeki, & Frackowiak, 1998; Leopold et al., 2002; Leopold & Logothetis, 1999).

Neuroscientific evidence indicates that neural activations during MIB as well as BR occur at multiple sites. For example, in functional magnetic resonance imaging (fMRI) studies it was shown that hemodynamic blood-oxygen-dependent level (BOLD) signals correlated with target disappearance during MIB. Multiple retinotopic subregions corresponded to processing of target and mask attributes in visual cortical areas V1 through V4 (Donner, Sagi, Bonneh, & Heeger, 2008; Libedinsky, Savage, & Livingstone, 2009; Schölvinck & Rees, 2009). Interestingly, Donner et al. (2008) found little evidence for BOLD response modulation around the time of the subjective target disappearance in early visual areas V1 through V3, suggesting that target disappearance may emerge at a later stage of visual processing. More specifically, BOLD activity in ventral visual area V4, corresponding retinotopically to the target, decreased with motion-induced disappearance of the target. At the same time, activity in mask-specific dorsal visual areas increased when the target disappeared, suggesting an antagonistic interplay between representations of the moving mask and the stationary target confined to different neural sites in the visual processing stream. Libedinsky et al. (2009) as well as Schölvinck and Rees (2009), on the other hand, reported systematic modulations of neural activity in V1 in correspondence with key presses for target disappearances.

More recently, Donner, Sagi, Bonneh, and Heeger (2013) investigated correlations between time series of fMRI activity in multiple retinotopic subregions corresponding to target and mask in MIB. They reported spatial patterns of fluctuations that reflected the duration and rate of MIB and showed retinotopic specificity for the target, but in distinct cortical areas: Fluctuations of neural activity in V1 reflected phase durations of target disappearances, whereas fluctuations of activity in V4 reflected the rate of target disappearances. This suggests that local sensory characteristics of the target may affect phase durations at an earlier level, whereas global mask attributes may affect rates at later stages of processing.

Neuroimaging studies on BR have shown that the strength of neural representation of a target stimulus in ventral visual cortex V1 is linked to observers' perception of that target during BR (Lee, Blake, & Heeger, 2005; Meng, Remus, & Tong, 2005; Polonsky, Blake, Braun, & Heeger, 2000; Tong & Engel, 2001) and even correlates with perceived stimulus rivalry in visual areas as early as *Lateral geniculate nucleus* (LGN) (Haynes, Deichmann, & Rees, 2005; Wunderlich, Schneider, & Kastner, 2005). However, conflicting findings on the neural underpinnings of BR led to the suggestion that, depending on the specific stimulus attributes, BR may occur and influence multiple sites distributed within the visual processing hierarchy (Blake & Logothetis, 2002; Bonneh, Sagi & Karni, 2001b; Lee et al., 2007; Tong, Meng, & Blake, 2006).

This idea has also been advanced in computational models that involve at least two processing stages (Freeman, 2005; Gigante, Mattia, Braun, & Del Giudice, 2009; Wilson, 2003). These hierarchical models suggest competition between higher-level binocular representations of images ("object rivalry") in addition to reciprocal inhibition between monocular representations of images tied to signals from each eye separately ("eye rivalry"). Wilson (2003) further proposed that neural competition may be a general characteristic that can be found throughout the levels of cortical visual processing and that inhibitory computations might operate at different levels of visual processing, thus helping to explain similar temporal dynamics in diverse sets of multistable phenomena (Arnold, 2011; Blake, 1989; Lehky, 1988; Leopold & Logothetis, 1999; Noest, van Ee, Nijs, & van Wezel, 2007).

In two experiments we investigated whether fluctuations among several perceptual states linked to BR and MIB are related. Thereto, we introduced binocular color rivalry (BCR) in a target dot of a stimulus display that also elicited intermittently target disappearance or MIB. We assigned different colors to the target dot in the left and right eyes because color fluctuations in a dichoptic target are easy to report, even when the target is small. In Experiment 1 we systematically manipulated target size together with two attributes of the mask to change target disappearances in MIB, and in Experiment 2 we varied luminance contrast of the dichoptic target to manipulate color appearances in BCR. We monitored phase durations of color appearance (BCR) and disappearance of the target (MIB) throughout each trial and compared temporal characteristics of each of the perceptual states of the target across conditions.

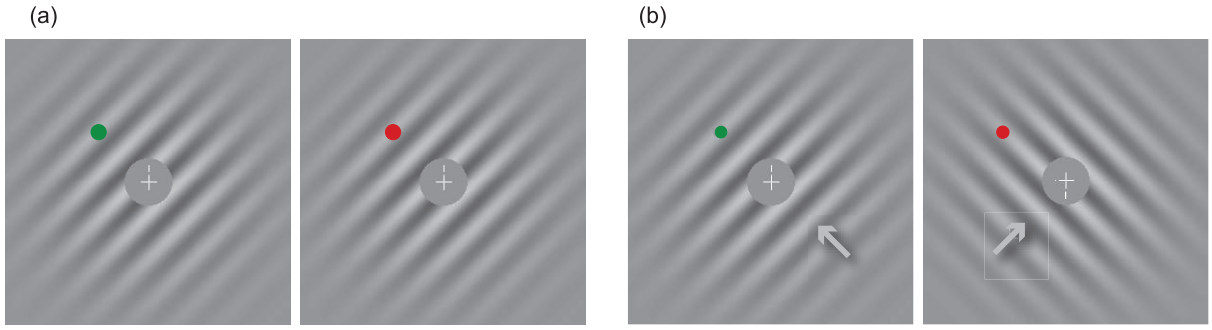

Figure 1. Experiment 1: Illustration of left and right eye stimulus display with (a) medium-sized target and nonrivalrous static grating and (b) small-sized target and drifting gratings in BR.

Following up on the neuroscientific evidence for MIB (Donner et al., 2013) and BR (Lee et al., 2007), we investigated whether MIB and BCR in the same local target leads to corresponding temporal fluctuations of perceptual states. Since the multistable percepts in the present paradigm are mutually exclusive, their accumulated or total durations are not independent. As a consequence a decrease in total disappearance, for example, will necessarily lead to an increase of total color appearances. However, a single oscillator (Carter & Pettigrew, 2003) or common inhibitory mechanism for MIB and BR (van Loon et al., 2013) would further predict that a systematic change in the dynamics of one phenomenon should be reflected by corresponding changes in the other (and vice versa). More specifically, a systematic reduction of phase durations of disappearance should lead to a corresponding change in phase durations of color appearances, whereas a systematic increase in phase durations of color appearances should systematically affect disappearances. Similarly, a systematic increase in rate or number of disappearances should trigger a corresponding change in number of color appearances.

Alternatively, if MIB and BR do not rely on a single mechanism then we cannot expect corresponding effects between the dynamics of disappearance and color appearances. More specifically, a shortening of phase durations for target disappearance would have no effect on the phase durations of color appearances. Similarly, it may be expected that an increase in the rate or number of disappearances should not change the number of color appearances.

If we assume mainly bottom-up processing in a hierarchical system, as suggested by neuroscientific evidence for MIB and BR (Donner et al., 2013; Lee et al., 2007), then we would expect that a changed phase duration of a percept at an earlier state (LGN, V1) should affect the rate of the same percept at a later stage (V2–V4). At the same time, however, a changed rate at a later stage may not affect phase durations. In addition, if top-down selective attention contributes to the mutually exclusive percepts in the present paradigm, we may anticipate systematic effects on perceptual stabilization—that is, reduced numbers of perceptual switches between color appearances interrupted by an intermittent disappearance (Brascamp & Blake, 2012; Brascamp et al., 2008; Leopold et al., 2002).

Experiment 1: Target size, mask motion, and mask rivalry

Each observer viewed the stimulus display with a dichoptic target dot superimposed on a (moving) mask (Figure 1a). During each trial the observer reported red and green color appearance and disappearance of the target by pressing and releasing color-coded keys.

In a within-subjects factorial design we varied local and global attributes of the stimulus. We hypothesized that local target size should systematically affect MIB in terms of phase durations, whereas global mask motion and mask rivalry may affect number of disappearances (Donner et al., 2013). These changes are also reflected in the total target color appearance and disappearance and should produce matching patterns in number and phase durations if both phenomena are governed by a common mechanism.

Methods

Participants

A total of 18 observers, undergraduate students from Glasgow University who were naïve to the aims of the experiment, took part in Experiment 1 (mean age = 22 years; six males). Four participants were excluded from analyses and results because one participant misunderstood the instructions and three participants reported very few disappearances (less than a single occurrence per trial). Each participant had normal or corrected-to-normal visual acuity without binocular (Random E test; Heron & Lages, 2012) or color

deficiencies. The experiment was approved by the Faculty Ethics Committee at University of Glasgow in agreement with the Declaration of Helsinki ethics guidelines. All participants gave informed written consent before taking part.

Apparatus and stimuli

Stimuli were generated in MatLab (MathWorks, Natick, MA) using Psychtoolbox extensions (Brainard, 1997; Pelli, 1997), run on a Macintosh G4 computer (Apple, Inc., Cupertino, CA), and presented stereoscopically on a calibrated Iiyama 21-in. Cathode-ray tube (CRT) monitor (resolution of 1024 × 768 pixels, refresh rate 120 Hz) in a split-screen Wheatstone configuration using haploscopic mirrors. The viewing distance was set to 114 cm. A chin and forehead rest (UHCO, Houston, TX) stabilized observers' viewing position.

The stimulus subtended approximately 5.6° × 5.6° and consisted of a mask: a white fixation cross flanked by nonius lines and a dichoptic target dot. The dichoptic target dot was red and green and was displayed 1.0° above and 1.0° to the left of the fixation cross projecting onto corresponding peripheral positions in the left and right eyes (Figure 1).

We presented the dichoptic target with different color at corresponding positions in the left and right eyes. The red (CIE x = 0.626, y = 0.342) and green (CIE x = 0.285, y = 0.613) circular target dot was rendered physically isoluminant at 18.7 cd/m^2 (ColorCal, Cambridge Research Systems, Rochester, UK). The target dot varied in size (small, medium, large), assuming a visual angle of 14.5, 19.0, and 23.7 arcsec.

The surrounding mask was a drifting or static sine wave grating with spatial frequency of 1.6 cycles/deg presented in a circular Gaussian window with 25% Michelson contrast at its peak (Figure 1a). Grating and gray surround had an average luminance of 18.7 cd/m^2. The grating mask remained static or appeared to move diagonally up or down, orthogonal to the orientation of the grating at 45° or 135°. In a condition with BR in the mask, the grating was presented with orthogonal orientation (and motion direction) in the left and right eyes (Figure 1b).

Design and procedure

The stimulus presentation was designed to elicit three easily distinguishable perceptual states of the target: red (R) or green (G) target appearance, and target disappearance (D).

We studied these perceptual states in a factorial design within subjects, combining target size (small, medium, large), mask motion (static, drifting), and mask rivalry (rivalrous, nonrivalrous) as independent variables. Participants attended a single session lasting between 35 and 45 min. Individual data were collected from each observer in a black room with lights switched off. A single session in Experiment 1 consisted of four blocks of 12 trials with target color in the left and right eyes and target size randomly intermixed across trials. The four blocks corresponded to presenting the mask in rivalry or not, and with the mask moving or static. The conditions with static masks were always presented first in order to avoid motion aftereffects in subsequent blocks (Lages, Adams, & Graf, 2009).

During each trial, the observer fixated a hairline cross with flanking nonius lines at the center of the display while attending to the target dot. The observer viewed the stimulus display for 30 s and reported the perceived color of the target by pressing and holding color-coded keys on the keyboard, similar to a standard BR task. The observer indicated color reversals by switching between the two keys. In addition, the observer indicated disappearance of the target dot by releasing both keys.

We monitored the three perceptual states in terms of total duration, number, and phase duration per trial. Note that the total phase duration equals the product of number and mean phase duration for each perceptual state. Total phase duration also reflects the mutual exclusive nature of the multistable percepts. Number of phases—equivalent to the alternation rate in bistable phenomena—together with mean phase duration and the pooled phase distribution describe the temporal characteristics of each perceptual state (see the Appendix for further details).

It is well documented that MIB decreases with local target size (Bonneh et al., 2001a) and that global motion of the mask promotes MIB (Lages et al., 2009; Wallis & Arnold, 2009). As another factor of interest, we introduced binocular (motion) rivalry in the surrounding mask to test a possible effect of global mask rivalry on local color rivalry and disappearance of the dichoptic target.

Total appearance and disappearance of the target, as well as number and phase duration of each perceptual state (R, G, D), varied considerably across observers. In order to reduce interindividual variability, we normalized the three dependent variables (total, number, and phase duration) of each perceptual state and observer. We conducted separate analyses on total, number, and phase duration of each perceptual state to obtain an overview of effects as well as the dynamics for each percept. We also pooled normalized phase durations across observers to increase the number of observations and fitted gamma distributions to the phase durations of each perceptual state. These fits illustrate differences between phase duration distributions across the main conditions.

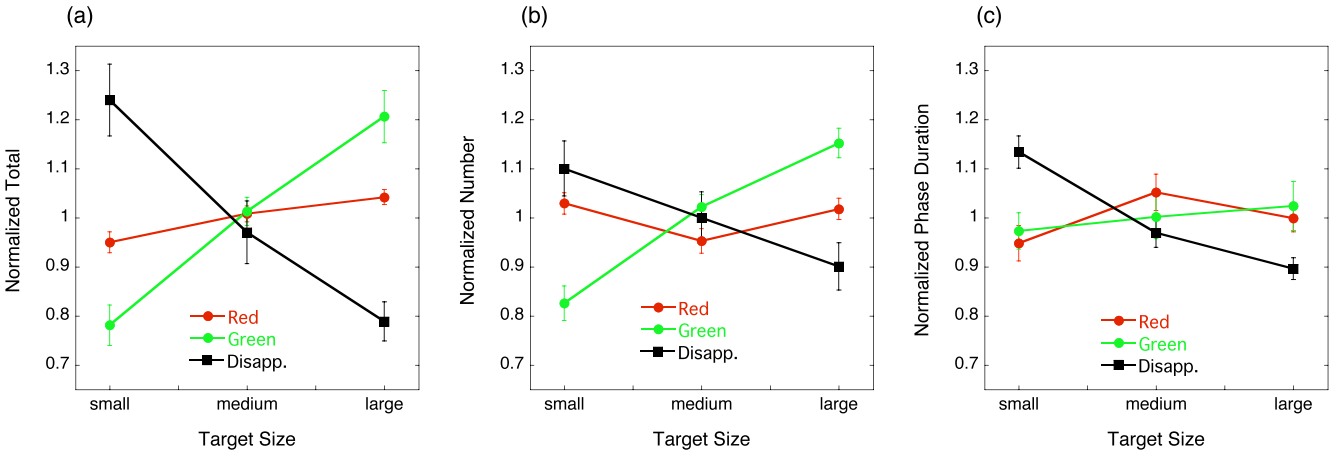

Figure 2. Experiment 1: Plots for normalized (a) total, (b) number, and (c) phase duration of red target appearance (red dots), green target appearance (green dots), and target disappearance (black squares) in trials with small, medium, and large targets. Error bars denote ±1 standard error of the mean (*SEM*).

Results

In a three-way multivariate analysis of variance (MANOVA) with repeated measures on factor target size (small, medium, large), motion of the mask (static, moving), and rivalry in the mask (parallel, orthogonal), we first analyzed the normalized total duration of each perceptual state to establish the effects on mutually exclusive percepts across conditions. This was followed by separate MANOVAs on normalized number and mean phase duration to capture temporal characteristics of each perceptual state. In the following we report only univariate test results and effect sizes.

Target size

We successfully replicated the effect of target size on disappearance (Bonneh et al., 2001a) and observed reduced total disappearance with target size, $F(2, 26) = 9.31$, $p < 0.001$, $\eta_p^2 = 0.417$. Total red target appearances, $F(2, 26) = 4.78$, $p = 0.017$, partial $\eta^2 = 0.269$, as well as total green target appearances, $F(2, 26) = 16.98$, $p < 0.0001$, partial $\eta^2 = 0.566$, increased significantly for larger targets, as may be expected for mutually exclusive events (Figure 2a).

The analyses on number and mean phase duration conveyed different effects for color appearances and target disappearance (Figure 2b, c). Interestingly, the reduced total disappearance for increasing target size did not significantly change the number of disappearances, $F(2, 26) = 2.36$, $p = 0.114$, but gave rise to significantly shorter phase durations, $F(2, 26) = 11.98$, $p < 0.001$, partial $\eta^2 = 0.480$. The increase of total red and total green appearance, on the other hand, was driven by a significant increase in number of green target appearances, $F(2, 26) = 19.57$, $p < 0.0001$, partial $\eta^2 = 0.601$, but not red target appearances, $F(2, 26) = 2.11$, $p = 0.142$. Unlike target disappearance, mean phase durations for red, $F(2, 26) = 1.59$, $p = 0.22$, and green target appearance ($F < 1$) were not significantly affected by target size.

These results suggest that increasing target size systematically shortened phase duration of target disappearances (Bonneh et al., 2001a). At the same time, this increased the number of green target appearances but did not significantly alter red and green phase durations, as shown in Figure 2c.

Distribution fits

These results were confirmed by gamma distribution fits to normalized phase durations of each perceptual state and target size pooled across observers (for details see Data analysis in the Appendix). The probability density distributions for normalized red (R), green (G), and disappearance (D) phase durations of the target are illustrated in Figure 3, with target disappearances (black) plotted on the negative axis for ease of comparison. Note that the observation of different phase distributions for red and green color appearances as well as disappearances in the present paradigm implies that suppression of target color and suppression of the target is based on different stochastic processes.

It is also clear that despite normalization, changes in the gamma distributions are not equivalent for the different perceptual states. Maximum-likelihood (ML) fits gave estimates of shape and scale parameters that indicated small but systematic changes for target disappearance but without corresponding effects for red and green target appearance (see parameter estimates in Table 1). Although the distribution fits give a detailed picture of the distribution of phase durations, they are based on normalized data for each perceptual state and observer and therefore do not

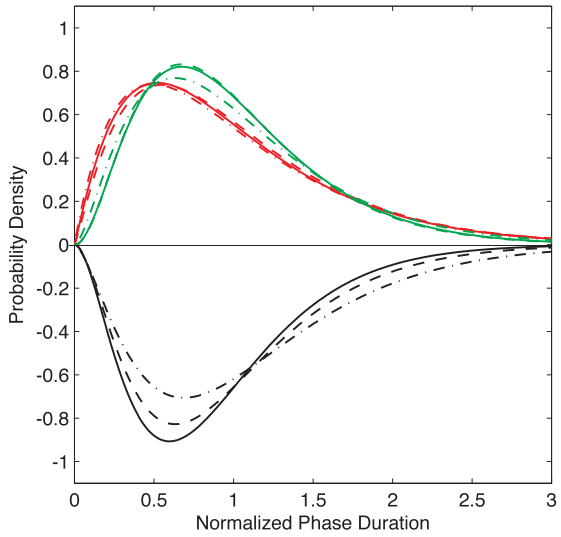

Figure 3. Experiment 1: ML fits of gamma distribution for small (dot-dashed), medium (dashed), and large (solid) target size. Probability density for red target appearance (red curves) and green target appearance (green curves) is plotted on the positive y-axis, and target disappearance (black curves) is plotted on the negative y-axis.

capture changes in total duration or number of occurrences. Mean durations in seconds and total numbers pooled over participants are provided in Table 2.

Mask motion

We also compared target disappearance with color appearance in conditions where the mask was static or moving. Again, in line with previous results (Bonneh et al., 2001a; Lages et al., 2009), total disappearance of the target increased significantly when the mask was in motion, $F(1, 13) = 7.12$, $p = 0.019$, partial $\eta^2 = 0.354$. As illustrated in Figure 4a, there was a small but statistically significant decrease of total red target appearance, $F(1, 13) = 5.61$, $p = 0.034$, partial $\eta^2 = 0.302$, when the mask was in motion but this time no corresponding change for total green appearance ($F < 1$).

The analyses on number and phase duration revealed a significant increase in number of red target appearance, $F(1, 13) = 6.70$, $p = 0.023$, partial $\eta^2 = 0.340$, and green target appearance, $F(1, 13) = 5.88$, $p = 0.031$, partial $\eta^2 = 0.311$, and at the same time a significant reduction in red phase duration, $F(1, 13) = 9.4$, $p = 0.010$, partial $\eta^2 = 0.419$, and green phase duration, $F(1, 13) = 5.4$, $p = 0.037$, partial $\eta^2 = 0.293$, when the mask was in motion. Unlike the manipulation of target size, target disappearance showed a statistically significant increase in number, $F(1, 13) = 12.24$, $p = 0.004$, partial $\eta^2 = 0.485$, but no change in phase duration ($F < 1$) when the mask was moving.

Although mask motion significantly increased number of appearances in the same way as disappearances (Figure 4b), only the phase durations for red and green target appearance were systematically reduced (Figure 4c). The ML fits of the gamma distribution to phase durations pooled across repeated trials and observers revealed an effect of mask motion on the shape parameter of red appearances only (Figure 5; Tables 1 and 2).

Mask rivalry

Contrary to our expectations, we found no significant effect of binocular mask rivalry on disappearance and relatively little effect on color appearance. Except for total green appearance, $F(1, 13) = 7.61$, $p = 0.016$, partial $\eta^2 = 0.369$, and number of red appearance, $F(1, 13) = 5.44$, $p = 0.036$, partial $\eta^2 = 0.295$, there were no statistically significant effects. This may indicate that BR in the mask, as a result of orthogonal orientation of the grating in the left and right eyes, had no effect on disappearance of the target and only nonspecific effects on BCR (Figure 6).

Experiment 1		Target size			Mask motion		Mask rivalry	
Level	Estimate	Small	Medium	Large	Static	Moving	Nonrivalrous	Rivalrous
Red (R)	α	1.99	2.19	2.1	2.08	2.4	2.04	2.28
	β	0.5	0.46	0.47	0.48	0.42	0.49	0.44
	μ	1	1.01	0.99	1	1	1	1
Green (G)	α	2.64	3.13	3.09	3.02	3.14	3.13	3.04
	β	0.39	0.32	0.32	0.33	0.32	0.32	0.33
	μ	1.03	1	0.99	1	1	1	1
Disappearance (D)	α	2.63	2.88	3	2.73	2.93	3.07	2.55
	β	0.42	0.34	0.3	0.37	0.34	0.33	0.39
	μ	1.1	0.98	0.9	1	1	1.01	0.99

Table 1. Experiment 1: ML estimates of shape α and scale β parameter (normalized $\mu = \alpha \times \beta$) of gamma distributions for the three perceptual states (normalized R, G, and D phase durations pooled across observers) and main conditions (target size, mask motion, mask rivalry).

Experiment 1		Target size			Mask motion		Mask rivalry	
Level	Statistic	Small	Medium	Large	Static	Moving	Nonrivalrous	Rivalrous
Red (R)	$\bar{x}$	2.94	3.03	2.94	3.37	2.62	2.88	3.06
	N	1,099	1,130	1,198	1,588	1,839	1,767	1,660
Green (G)	$\bar{x}$	2.16	2.08	2.04	2.3	1.9	1.96	2.2
	N	587	757	890	1,044	1,190	1,064	1,170
Disappearance (D)	$\bar{x}$	1.82	1.51	1.42	1.59	1.61	1.54	1.67
	N	814	701	630	946	1,199	1,176	969

Table 2. Experiment 1: Mean $\bar{x}$ of phase durations (in seconds, not normalized) and total number (*N*) of perceptual states (R, G, and D pooled across observers) for main conditions (target size, mask motion, mask rivalry).

However, ML fits of the gamma distribution to normalized phase durations pooled across repeated trials and observers suggest an opposite influence of mask rivalry on the shape parameter for disappearances (black lines) as well as red appearances (Figure 7; Tables 1 and 2).

Interactions

The two-way interaction between mask rivalry and target size for total red target appearance, $F(2, 26) = 3.89$, $p = 0.033$, partial $\eta^2 = 0.230$, and a three-way interaction between target size, mask motion, and mask rivalry for number of green target appearances reached statistical significance, $F(2, 26) = 3.88$, $p = 0.034$, partial $\eta^2 = 0.230$. Since we did not specify any hypothesis concerning interactions, we suggest that manipulation of local target size and global mask attributes affected the multistable percepts more or less independently (Alais & Parker, 2006; Carlson & He, 2004; Livingstone & Hubel, 1998). However, this may be the result of the specific stimulus attributes used in the present stimulus display (Graf & Adams, 2008; Graf, Adams, & Lages, 2002).

Perceptual stabilization

Previous studies have reported stabilization of the dominant percept during rivalry when the stimulus presentation was interrupted by a blank display or MIB (Leopold et al., 2002). Stabilization was expressed in terms of a significant increase in relative frequency or survival rate for the dominant percept interrupted by an intermittent disappearance or blank stimulus display.

We also computed survival rates for target colors interrupted by a target disappearance (Brascamp et al., 2008; Leopold et al., 2002). The survival rates for red and green target color were computed as the number of RDR and GDG transitions divided by the total number of all transitions per condition (red-disappearance-red [RDG] + GDR + RDR + green-disappearance-green [GDG]). Figure 7 shows the survival rates for target size and mask motion from Experiment 1 and for contrast from Experiment 2. Since BR in the mask did not significantly affect target disappearance, survival rates for mask rivalry are not shown.

An analysis with repeated measures on survival rates of red appearances, expressed as number of RDR transitions divided by the number of all possible transitions per condition, showed significant stabiliza-

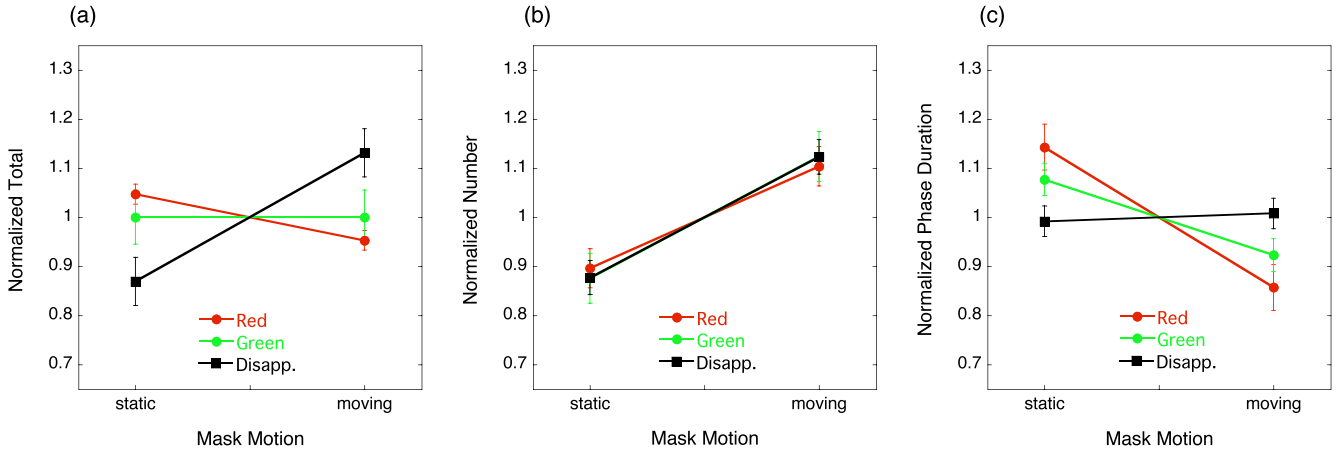

Figure 4. Experiment 1: Plots for normalized (a) total, (b) number, and (c) phase duration for red target appearance (red dots), green target appearance (green dots), and target disappearance (black squares) for trials with static and moving mask. Error bars denote ±1 *SEM*.

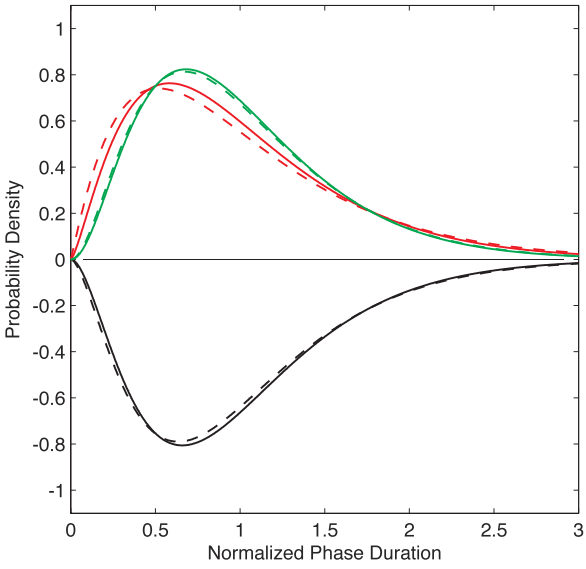

Figure 5. Experiment 1: ML fits of gamma distribution for static (solid) and moving (dashed) mask. Probability density for red target appearance (red curves) and green target appearance (green curves) is plotted on the positive y-axis, and target disappearance (black curves) is plotted on the negative y-axis.

tion for dominant red color appearance (Figure 8a; Leopold et al., 2002). With increasing target size the red survival rate was significantly reduced, $F(2, 26) = 9.1$, $p = 0.002$, partial $\eta^2 = 0.410$. The opposite effect—a small and just significant increase for green survival rates, $F(2, 26) = 4.23$, $p = 0.048$, partial $\eta^2 = 0.245$—was also observed (Brascamp et al., 2008). However, despite increased target disappearance for a moving mask, no significant changes of red and green survival rates were observed for trials with static and moving mask (Fs < 1; Figure 8b).

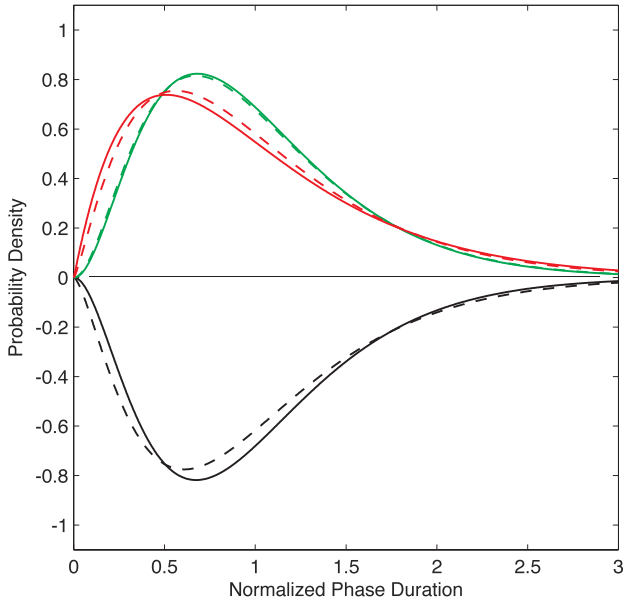

Figure 7. Experiment 1: ML fits of gamma distribution for nonrivalrous (solid) and rivalrous (dashed) mask. Probability density for red target appearance (red curves) and green target appearance (green curves) is plotted on the positive y-axis, and target disappearance (black curves) is plotted on the negative y-axis.

Discussion

We successfully replicated the effect of target size and mask motion (Bonneh et al., 2001a) on target disappearance in the present paradigm. More specifically, we found that increasing target size reduced phase duration of disappearances and increased number of green phases. Within the same paradigm, mask motion increased number of disappearances as well as number of red and green appearances while

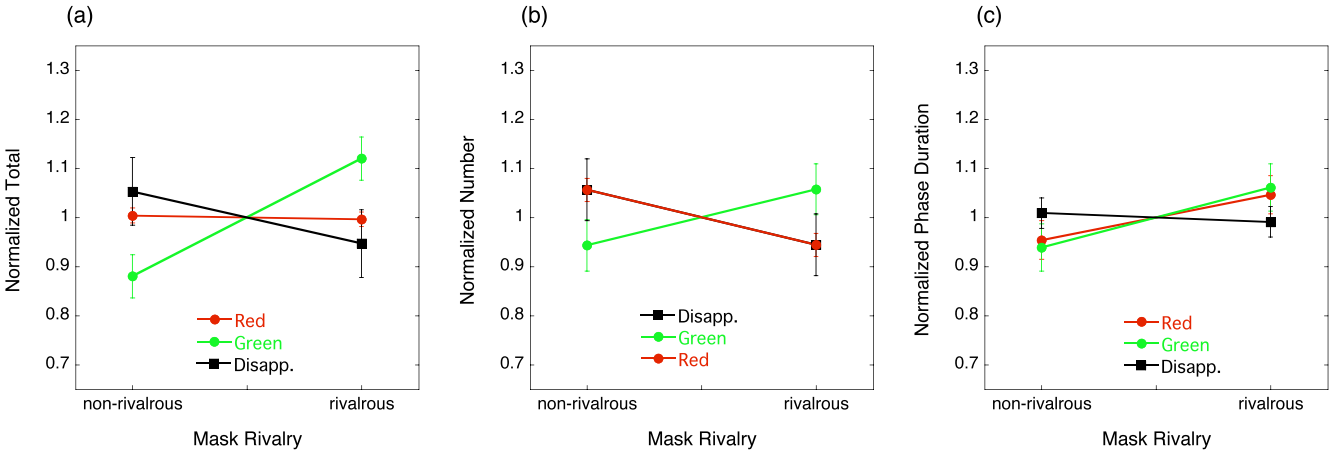

Figure 6. Experiment 1: Plots for normalized (a) total, (b) number, and (c) phase duration for red target appearance (red dots), green target appearance (green dots), and target disappearance (black squares) for trials with nonrivalrous and rivalrous mask. Symbols represent values averaged across participants, and error bars denote ±1 *SEM*.

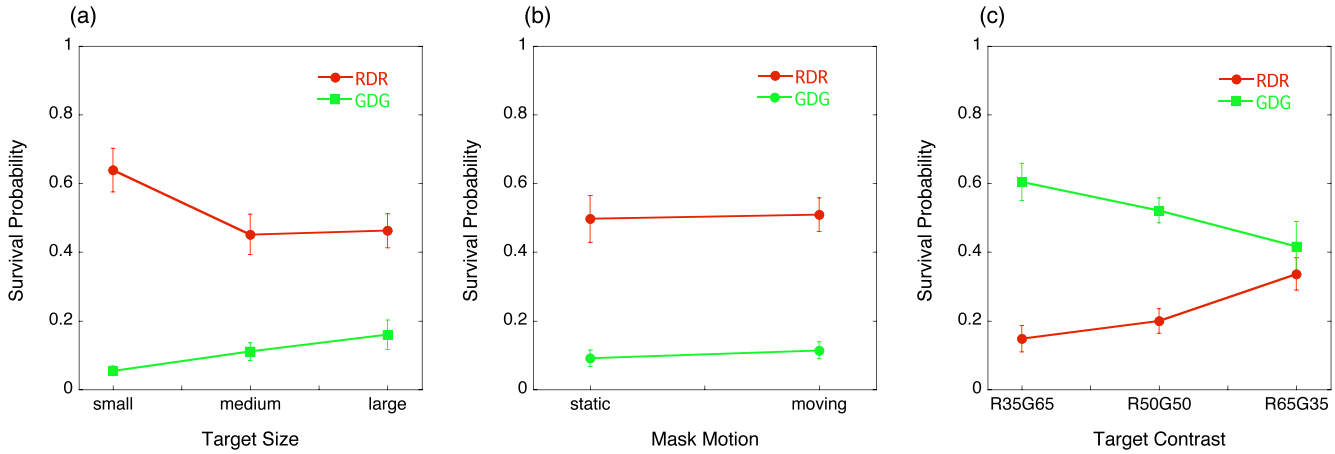

Figure 8. Survival rates averaged across participants for red (RDR) and green (GDG) color appearance of the target interrupted by a disappearance for (a) target size in Experiment 1, (b) mask motion in Experiment 1, and (c) target contrast in Experiment 2. Error bars denote ±1 *SEM*.

shortening green and especially red phase durations. However, this did not significantly affect mean phase durations of disappearances. In addition, mask rivalry had an effect on number of red appearances. This altered the shape of the distribution for red appearances, whereas the distribution of target disappearances showed an opposite trend. In summary, the results suggest that perceptual states linked to BCR and MIB are differently influenced by target size and mask motion, but not necessarily by mask rivalry.

Our manipulation of target size significantly shortened phase durations but did not increase number of disappearances, whereas manipulation of mask motion significantly increased number but did not modulate phase durations of disappearances. According to Donner et al. (2013), this would suggest that target size modulated neural activity in V1 whereas mask motion predominantly affected neural activity in V4, possibly reflecting processing of local target and global mask attributes of the stimulus at different stages in the visual hierarchy.

Mask motion in our stimulus may be interpreted as a global surface attribute, facilitating surface completion (Bakin, Nakayama, & Gilbert, 2000) and thereby increasing target disappearances (Graf et al., 2002). At the same time, however, the drifting grating around the target may have induced modulation of color contrast in the local target (De Valois, Webster, De Valois, & Lingelbach, 1986), affecting BCR. In the framework of hierarchical processing, mask motion as a global surface attribute may increase number but not phase durations of disappearances (Donner et al., 2013). On the other hand, if mask motion also induced contrast modulation in the local target, then this may have decreased red and green phase durations at an early stage of processing (LGN, V1) and possibly number of red and green phases at a subsequent stage of processing.

The corresponding trends for number of target disappearance and color appearance may suggest coupled activity at later processing stages, whereas the noncorresponding phase durations for target disappearance and color appearance may suggest relatively independent activity at earlier processing stages. For instance, number of disappearances tends to correspond with the number of one (or both) color appearance, whereas phase durations of disappearances do not correspond with phase durations of color appearances. We therefore suggest that MIB and BCR in this experiment responded differently to manipulations of local and global attributes in the stimulus.

Mask rivalry in the present display was a relatively global attribute of the stimulus and affected only number of red target appearances. Interestingly, mask rivalry did not significantly affect number or phase durations of the target disappearance but altered the gamma distribution for disappearances pooled across observers.

Importantly, however, effects on the dynamics of MIB and BCR were incoherent for other manipulations of stimulus attributes, suggesting different processing for MIB and BCR—most likely at different stages within the visual system.

In addition, survival rates for dominant red target appearances indicated stabilization, with increasing disappearance for smaller targets. Reduced reversals and increased stabilization have been related to top-down processing and selective attention (Leopold et al., 2002). Here, we observed not only a significant increase of survival rates for dominant red target appearance but also a small reduction for green target appearance (Brascamp et al., 2008). Interestingly,

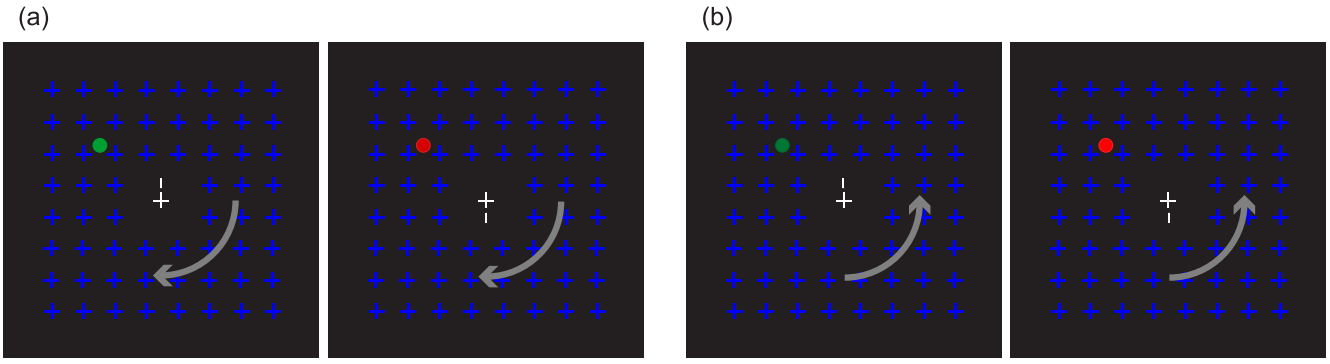

Figure 9. Experiment 2: Illustration of left and right eye stimulus display with (a) isoluminant dichoptic target (R50:G50) and counterclockwise rotating matrix of crosses and (b) nonisoluminant dichoptic target (R65:G35) and clockwise rotating matrix of crosses.

although mask motion increased target disappearances, we found no stabilization effect on survival rates for color appearances in trials with a moving mask (Figure 8b).

In Experiment 2 we used an array of crosses on a black background, typically employed in MIB studies, as the mask in order to increase the number of disappearances per trial. We also manipulated a stimulus characteristic that is known to affect BCR. By changing luminance contrast in the dichoptic target we expected systematic changes in red and green target appearance (Levelt, 1965). If a single oscillator or common inhibitory mechanism governs color appearances and disappearances, then increased strength of the dominant color should not only decrease the phase duration of the opposite color appearance but also systematically alter the phase duration of disappearances. However, if BCR and MIB are based on different processing, then a change in phase durations of color appearances may not affect phase durations of disappearances.

Experiment 2: Target contrast

We manipulated luminance contrast in the dichoptic target (Blake, 1977; Levelt, 1965; Mueller & Blake, 1989) embedded within a global rotating mask and studied how target contrast affected color appearance and disappearance of the local target. Luminance of the red target in one eye was increased from 50% to 65% (or decreased from 50% to 35%) while luminance of the green target in the other eye was decreased from 50% to 35% (or increased to 65%) accordingly. In a control condition both target colors remained at 50% in the left and right eyes. It is well documented that an increase in luminance of an image in one eye suppresses the image in the other eye (Levelt, 1965), but it is unknown whether and how this affects target disappearance in the same stimulus.

Methods

Participants

A total of 12 observers (mean age = 23 years; five males), undergraduate students from Glasgow University and naïve to the aims of the experiment, took part. Each participant had normal or corrected-to-normal visual acuity without binocular or color deficiencies. The experiment had the same ethical approval as Experiment 1.

Apparatus and stimuli

Stimuli were displayed using the same equipment as in Experiment 1. The stimulus subtended approximately 5.6° × 5.6° and consisted of a black background, a rotating mask, a white fixation cross flanked by nonius lines, and a dichoptic target dot. The mask consisted of an 8 × 8 grid of blue crosses that rotated clockwise or counterclockwise at 30°/s around the fixation cross (Figure 9).

The dichoptic target dot subtended 14.5 arcsec and was presented in red and green at corresponding positions 1.0° above and 1.0° to the left of the fixation cross in the left and right eyes. We varied luminance contrast by setting red and green target luminance to 8.9 cd/m^2, 12.7 cd/m^2, or 16.6 cd/m^2, so that monocular contributions were 35%, 50%, or 65%, respectively. The resulting conditions are labelled R35:G65, R50:G50, and R65:G35.

Design and procedure

As before, the stimulus display was designed to elicit three perceptual states: red target appearance (R), green target appearance (G), and target disappearance

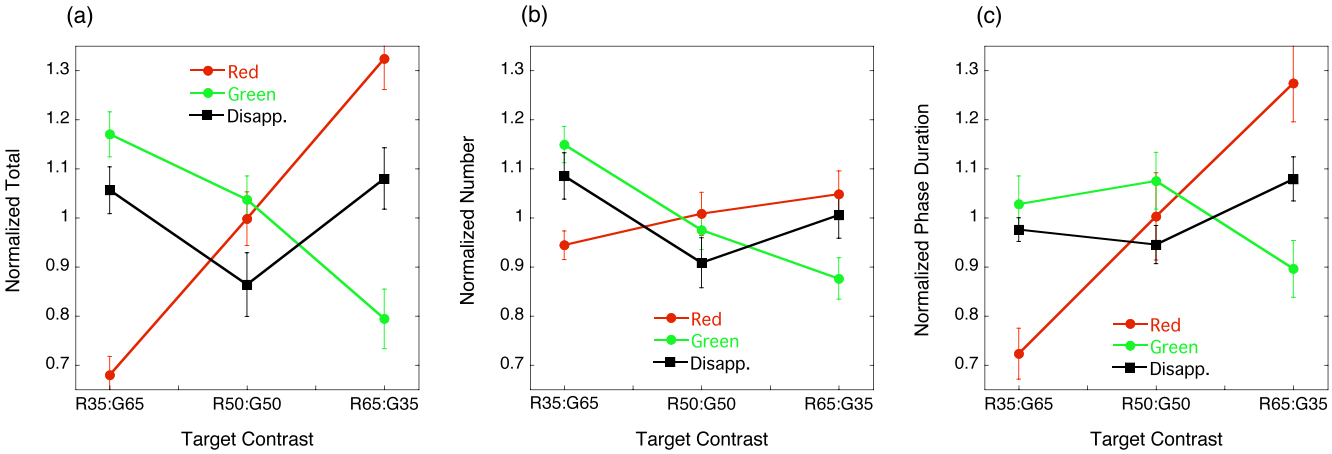

Figure 10. Experiment 2: Plots of normalized (a) total, (b) number, and (c) phase duration for red target appearance (red dots), green target appearance (green dots), and target disappearance (black squares) for luminance contrasts in the dichoptic target (R35:G65, R50:G50, and R65:G35). Symbols are values averaged across participants, and error bars denote ±1 *SEM*.

(D). We studied the three perceptual states in a within-subject design varying luminance contrast between the red and green target dot presented to the left and red eyes. Participants attended a single session lasting between 35 and 45 min. Individual data were collected from each observer in a black room with lights switched off. In two blocks of 12 trials the dichoptic target dot was shown with three different luminance contrasts between the left and right eyes. We used physical isoluminance because subjective isoluminance (Lu, Lesmes, & Sperling, 1999) is difficult to establish and was not essential here. Color of the target in the left and right eyes (red, green), color contrast (R35:G65, R50:G50, R65:G35), and direction of mask rotation (clockwise, counterclockwise) were randomly intermixed across trials. Each trial lasted 60 s; otherwise, the procedure was the same as in Experiment 1.

Results

Similar to Experiment 1 we conducted separate MANOVAs on total as well as number and phase duration for each perceptual state (R, G, D) to obtain an overview of effects on temporal fluctuations. Again, we pooled normalized phase durations across observers to increase the number of observations. We then fitted gamma distributions to the phase durations of each perceptual state. These fits illustrate differences between distributions of phase durations across the main condition.

In a MANOVA with repeated measures on the factor target contrast (R35:G65, R50:G50, and R65:G35) we confirmed that luminance contrast significantly increased total appearance of the red target, $F(2, 22) = 24.5$, $p < 0.001$, partial $\eta^2 = 0.690$, and significantly decreased total appearance of the green target, $F(2, 22) = 8.9$, $p = 0.001$, partial $\eta^2 = 0.448$. The increased appearance of the red target was accompanied by significantly prolonged red phase durations, $F(2, 22) = 9.01$, $p < 0.001$, partial $\eta^2 = 0.450$, whereas the increase in green target appearance was mainly due to a significant increase in number of green appearances, $F(2, 22) = 8.1$, $p = 0.002$, partial $\eta^2 = 0.423$. Crucially, however, manipulating target contrast did not significantly affect target disappearance (Figure 10) in terms of total duration, $F(2, 22) = 2.68$, $p = 0.091$; number, $F(2, 22) = 2.23$, $p = 0.132$; and phase duration, $F(2, 22) = 2.37$, $p = 0.117$.

Distribution fits

The above results were confirmed by ML fits of the gamma distribution to the normalized phase durations of each percept (R, G, D). Despite normalization and pooling across observers, the gamma fits indicate distributions with different shape and scale parameters across conditions for each perceptual state (Figure 11; Tables 3 and 4). The probability density function for red phase durations changed dramatically for luminance contrast but less so for green phase durations. There was some variation for target disappearances across conditions, but this nonsignificant effect did not correspond to the manipulation of luminance contrast in the dichoptic target.

Perceptual stabilization

In additional analyses with repeated measures on survival rates of target colors, expressed as number of RDR and GDG transitions divided by the total number of all possible transitions per condition, we found significant stabilization for green survival rates as the dominant color percept (Leopold et al., 2002). However,

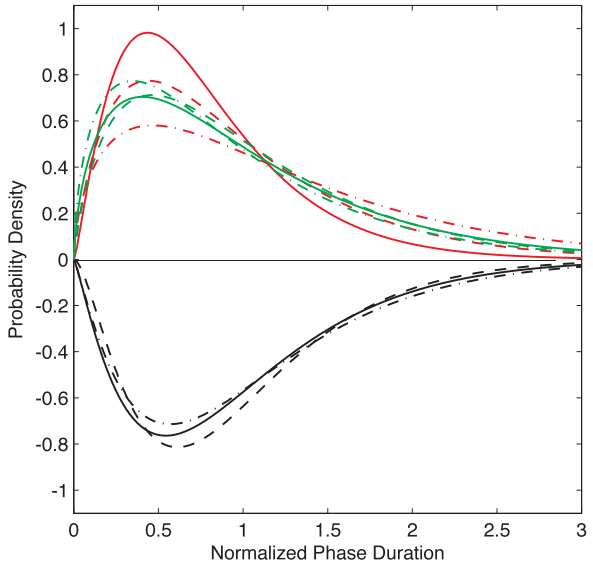

Figure 11. Experiment 2: ML fits of gamma distributions for R35:G65 (solid), R50:G50 (dashed) and R65:G35 (dot-dashed) luminance contrast in the dichoptic target. Probability density of red (red curves) and green (green curves) target appearance is plotted on positive and target disapperance (black curves) on negative y-axis.

green survival rates decreased with green target luminance, $F(2, 22) = 5.20$, $p = 0.014$, partial $\eta^2 = 0.321$, despite the absence of a systematic effect on disappearance (Figure 8c). The opposite effect—red survival rates increasing with red target luminance, $F(2, 22) = 10.14$, $p = 0.001$, partial $\eta^2 = 0.480$—was even more pronounced (Brascamp et al., 2008).

Discussion

We successfully replicated the well-known effect of dichoptic contrast in the current paradigm. A target dot with higher contrast in one eye strongly suppressed perception of a target dot with lower contrast in the other eye. However, this systematic effect for BCR was not reflected in number or phase duration of target disappearances and therefore MIB.

As predicted, changing luminance contrast in the dichoptic target had opposite effects on total red and total green target appearances. This general effect on BCR was mainly driven by decreasing numbers of green appearances and increasing red phase durations. Although target disappearance showed some variability across conditions, this trend was nonsignificant and did not match up with the effects on color appearance. Instead, the slightly reduced disappearance in the isoluminant condition (R50:G50) compared with both nonisoluminant conditions (R35:G65 and R65:G35) may indicate that a contrast-induced—and therefore more salient—red or green target in one eye facilitated target disappearance in both eyes (Grindley & Townsend, 1965, 1967; Jaworska & Lages, 2012; MacKay, 1960).

Experiment 2		Target contrast		
Level	Estimate	R35:G65	R50:G50	R65:G35
Red (R)	α	2.31	1.88	1.6
	β	0.33	0.51	0.78
	μ	0.77	0.94	1.25
Green (G)	α	1.65	1.83	1.59
	β	0.62	0.56	0.59
	μ	1.04	1.02	0.94
Disappearance (D)	α	2.24	2.71	2.19
	β	0.44	0.36	0.48
	μ	0.98	0.97	1.05

Table 3. Experiment 2: ML estimates of shape α and scale β parameter (mean $\mu = \alpha \times \beta$) of gamma distributions for the three perceptual states (normalized R, G, and D phase durations pooled across observers) and different luminance contrasts of the dichoptic target.

In the context of hierarchical processing in BR (Lee et al., 2007), a strong effect on phase durations probably involves early stages of processing (LGN, V1), whereas it is unclear whether an altered rate of percepts also relates to changed neural activity at a subsequent stage, as observed for MIB (Donner et al., 2013). Importantly, however, the effects on red phase durations and number of green appearances were not mirrored by target disappearances, again suggesting different temporal characteristics for BCR and MIB and therefore different processing within a hierarchical visual system.

Survival rates for red and green target appearance interrupted by disappearance (RDR, GDG) showed stabilization due to target contrast. Stabilization has been related to top-down processing and selective attention (Leopold et al., 2002), but the opposing effects of target contrast on survival rates for red and green color appearances are not accompanied by a change in target disappearance. This indicates a

Experiment 2		Target contrast		
Level	Stat	R35:G65	R50:G50	R65:G35
Red (R)	$\bar{x}$	2.18	2.79	3.6
	N	487	568	588
Green (G)	$\bar{x}$	3.67	3.77	3.56
	N	900	786	650
Disappearance (D)	$\bar{x}$	1.86	1.74	1.93
	N	659	580	612

Table 4. Experiment 2: Mean $\bar{x}$ of phase durations (in seconds, not normalized) and total number (N) of perceptual states (R, G, and D pooled across observers) for different luminance contrasts of the dichoptic target (R35:G65, R50:G50, R65:R35).

possible influence of sensory adaptation rather than selective attention on perceptual stabilization (Brascamp et al., 2008; Rose & Lowe, 1982).

In summary, the results of Experiment 2 show that perceptual states related to BCR and MIB are differently influenced by dichoptic contrast in the target. We found that target contrast mainly increased red phase durations and decreased number of green phases. Both effects were not mirrored by phase duration or number of target disappearances. This implies that MIB and BCR responded differently to the manipulation of local target contrast.

General discussion

A correlation between switch rates as reported by Carter and Pettigrew (2003) may simply reflect individual differences, such as the level of GABA neurotransmitters in inhibitory processing (van Loon et al., 2013) or the willingness of the observer to report a perceptual switch. Moreover, the gamma distribution is a powerful descriptive tool that accommodates a wide range of stochastic processes so that comparable distribution fits for MIB and BR phase durations provide limited evidence in favor of a common source for bistable and multistable percepts. We therefore believe that previously reported evidence is insufficient to postulate a single oscillator for both phenomena.

In the present experiments the distribution fits to normalized color appearances and disappearances showed systematic differences for various manipulations in the stimulus. Therefore, it seems reasonable to conclude that the underlying processes for BCR and MIB have changed. Although we are not in the position to say how and where exactly the underlying processes changed, the differences are pronounced enough to dismiss a common oscillator as the source of the systematic changes in our multistable percepts. In the following we speculate on alternative mechanisms and explanations.

If we interpret the results of Experiments 1 and 2 together, then the diverse pattern of effects on number and phase duration suggests that the perceptual states linked to BCR and MIB are not simply governed by a single oscillator (Carter & Pettigrew, 2003) or common inhibitory mechanism (van Loon et al., 2013). Instead, fluctuations in the target were differently modulated by local and global stimulus attributes. Although the phase durations of all three perceptual states can be described by gamma distributions, systematic changes of parameters across experimental conditions indicate that color rivalry in the dichoptic target and ambiguity between mask and target are resolved by processing at different levels within the visual hierarchy. Our behavioral results therefore supplement and strengthen previous neuroscientific evidence that neural activation during BR (Lee et al., 2007) and MIB (Donner et al., 2008, 2013) typically involves multiple neural sites in the visual hierarchy.

It appears plausible that local target attributes affect phase durations and, as a consequence, the number of percepts. However, any additional effects of local stimulus attributes on rate or number of perceptual states were specific for each percept rather than characteristic of the two phenomena investigated here. For example, target size significantly affected phase durations of disappearances (MIB) and only number of green phases (BCR), whereas target contrast modulated red phase durations and number of green phases (BCR) but not target disappearances (MIB).

The effects of intermittent blank periods on BR and other forms of bistable perception are at least qualitatively equivalent (Leopold et al., 2002) and the relationships between stimulus strength and alternation dynamics are comparable (Klink, van Ee, & van Wezel, 2008), suggesting a common computational but not necessarily neural mechanism. In the present experiments, the local attribute of target size influenced phase durations of MIB but not BCR. Conversely, changes in target contrast affected phase durations of BCR but not MIB. The more global attribute of mask motion did not affect phase durations of disappearances but only number of disappearances. However, phase duration of color appearances and number of color appearances were both affected by mask motion. In summary, stimulus-specific attributes seem to drive temporal characteristics of one phenomenon but not necessarily the other.

While processing of stimulus-specific attributes may occur at different stages within the visual system, the multistable percepts linked to BCR and MIB are mutually exclusive. They are likely to involve late selective attention, as suggested for BR (Brascamp & Blake, 2012; Ooi & He, 1999; Paffen, Alais, & Verstraten, 2006) and MIB (Bonneh et al., 2001a; Leopold et al., 2002). For example, systematic effects on phase durations during BR were reported when administering transcranial magnetic stimulation (TMS) to left and right parietal areas (Britz, Pitts, & Michel, 2011; Carmel, Walsh, Lavie, & Rees, 2010; Kanai, Muggleton, & Walsh, 2008; Zaretskaya, Thielscher, Logothetis, & Bartels, 2010). However, these results were inconsistent, possibly because different TMS paradigms (online/offline) in these studies triggered activation or inhibition in an extended network. Neural correlates of BR in prefrontal areas (Lumer, Friston, & Rees, 1998; Lumer & Rees, 1999) also suggest a top-down influence of selective attention, but these activities may be confounded by tasks where the observer has to monitor and report their own perceptual states (de

Graaf, de Jong, Goebel, van Ee, & Sack, 2011; Frässle, Sommer, Naber, Jansen, & Einhäuser, 2013; Knapen, Brascamp, Perason, van Ee, & Blake, 2011; Lages & Jaworska, 2012).

How exactly the two phenomena are organized in the visual system is difficult to unravel, as bottom-up (feedforward), lateral (cross-talk), and top-down (feedback) processing are likely to contribute to perceptual rivalry (Sterzer, Kleinschmidt, & Rees, 2009; Sterzer & Rees, 2008). This is further complicated by the suggestion that selective attention and visual awareness may represent different processing (Lamme, 2003; Watanabe et al., 2011). Nevertheless, it seems plausible that BCR in a small dichoptic target involves earlier processing stages (LGN, V1) than disappearance of the same target induced by a surrounding mask (V2–V4). Although we are convinced that switching between multistable percepts in the present paradigm also involves late processing in an attentional network, the diverse pattern of temporal characteristics suggests that these dynamics reflect sensory processing at earlier levels before top-down selective attention can exert an influence.

In Experiment 1 we observed perceptual stabilization of the dominant color (BCR) when target size increased intermittent disappearance durations (MIB). However, stabilization was also observed in Experiment 2 where color contrast had no corresponding effect on disappearance. Interestingly, in Experiment 1 mask motion had no effect on perceptual stabilization despite increased number of disappearances. Again, these diverse results suggest that in the present paradigm local rather than global stimulus-specific attributes had an effect on perceptual stabilization.

Assuming that BCR and MIB in the present experiments are examples of a wider class of multistable phenomena where different representations compete for visual awareness in a hierarchical system, it seems plausible that local and global stimulus attributes such as target size, mask motion, and target contrast significantly changed processing at different stages. As a consequence, fluctuations of MIB and BCR in the same target stimulus were differently affected by the same stimulus manipulations before reaching conscious awareness. It would be interesting to see whether our results for the combination of MIB and BCR can be extended to other phenomena of perceptual rivalry, especially to ambiguous stimuli that are under more attentional control (Grossmann & Dobbins, 2006; Leopold et al., 2002; Meng & Tong, 2004; van Ee, Noest, Brascamp, & van den Berg, 2006). This would raise the question of whether different characteristics in the multistable percepts reflect a (partial) dissociation between visual awareness and selective attention (Lamme, 2003; Watanabe et al., 2011). Furthermore, it may be argued that fluctuations of visual awareness as observed in the present paradigm do not rely on rhythmically synchronized activity in a unitary entity or network but rather are the result of complex and distributed processing in a modular and hierarchical system (Tong, 2003; Zeki, 2003; Zeki & Bartels, 1999). This would imply that rhythmically synchronized oscillation in a large-scale network, as typically observed in essentially bistable phenomena (e.g., Doesburg, 2009; Landau & Fries, 2012), is not necessarily the only neural correlate of visual awareness—especially for multistable phenomena.

Conclusions

In the present paradigm we manipulated local and global stimulus attributes and monitored effects on the dynamics of MIB and BCR competing for visual awareness. Although the multistable perceptual states showed comparable temporal characteristics, manipulation of stimulus attributes indicated differential processing, most likely at different levels within the visual system.

In two psychophysical experiments we have shown that disappearance and color appearance of a target respond differently to local target and global mask manipulations. This implies that MIB and BCR, when elicited in the same stimulus, are not simply the result of a single oscillator (Carter & Pettigrew, 2003) or a common inhibitory mechanism (van Loon et al., 2013). Instead, we suggest that MIB and BCR as well as other perceptual rivalries may follow similar computational principles but that processing that leads to fluctuations of visual awareness is likely to occur at different levels within a modular and hierarchical visual system (Blake & Logothetis, 2002; Meng & Tong, 2004).

Keywords: visual awareness, motion-induced blindness, binocular rivalry, multistable, gamma distribution, visual hierarchy

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Appendix

Data analysis

We recorded phase durations of each perceptual state (R = red, G = green, D = disappearance). The total was calculated by accumulating phase durations of matching states over a given trial. Number of a perceptual state is the number of occurrences of a percept during a trial, whereas phase duration refers to the mean duration between onset and offset of a percept during a trial. The initial interval from the onset of each trial and the first key press was excluded and only phase durations that lasted longer than 0.5 s were included in the analyses.

Total, number, and phase duration of each perceptual state were averaged across repeated trials but varied considerably across observers. In order to reduce interindividual variability and to facilitate comparison across conditions, we normalized the three dependent variables (total, number, phase duration) for each perceptual state (R, G, D) and observer before conducting further analyses.

Distribution fitting

A standard way of reporting temporal dynamics of BR and MIB is to fit a gamma distribution with two free parameters to a sample of phase durations (van Ee et al., 2006). Lognormal distributions with two free parameters gave consistently worse fits. In order to obtain reliable fits per condition we increased the number of observations by pooling normalized phase durations for each perceptual state across observers. We included only phase durations that lasted longer than 0.5 s to ensure that unintended delays or transitions between colors were not classified as perceptual states. The resulting data sets were fitted by a gamma distribution with two parameters of the form

$$f(x;\alpha,\beta) = \frac{1}{\beta^{\alpha}}\frac{1}{\Gamma(\alpha)}x^{\alpha-1}e^{\frac{-x}{\beta}},$$

where $\Gamma(\alpha)$ is the gamma function with $x \geq 0$, and $\alpha > 0$ is the shape and $\beta > 0$ the scale parameter. (Alternatively, the gamma distribution can be parameterized in terms of a shape parameter α and an inverse scale parameter $\theta = {}^{1}/_{\beta}$, called a rate parameter.) The shape parameter α characterizes the skewness of the distribution, whereas the scale parameter β scales the distribution along the abscissa.

Since phase durations were normalized for each observer, shape and scale parameter are linearly related across conditions with overall mean $E(x) = \mu = \alpha \times \beta = 1$. The parameter estimates for the main effects are presented in Tables 1 and 2 for Experiment 1 and in Tables 3 and 4 for Experiment 2. For a more sophisticated method and analysis of transient and sustained dynamics of bistable percepts, see, for exam3ple, Mamassian and Goutcher (2005).